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SIXTH REPORT.

RECENT PROGRESS IN PHYSIOLOGY.

By H. P. BOWDITCH, M. D.

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COURSE OF NERVE-FIBRES IN THE SPINAL CORD.

THE difficulties which attend an experimental inquiry into the channels by which sensitive and motor impressions traverse the spinal cord have been, to a great extent, surmounted in a recent investigation by Woroschiloff;[1] and the uniformity of the results obtained is so great as to justify the hope that an extension of the method adopted will finally give a satisfactory solution of this much disputed question. Previous observations by Miescher,[2] Nawrocki,[3] and Dittmar,[4] had shown that in rabbits the lateral columns of the spinal cord contain the nerve-fibres, both afferent and efferent, which are concerned in the production of a reflex contraction of blood-vessels, due to an irritation of the sciatic nerve. To ascertain whether the channels of reflex and voluntary movement of the muscles of the trunk and limbs lie also in the same region of the cord, Woroschiloff was compelled to modify in several respects the methods adopted by the above-named observers. In the first place, the necessity of observing the contractions of striped muscles forbade the use of curare to render the animal motionless, and yet absolute immobility of the spinal cord at the time of making the sections of the different parts — for this was the method of investigation adopted — was essential to the success of the experiment. This object was accomplished by means of a double clamp, which was screwed firmly upon the vertebral column above and below the point where the spinal canal was laid open by the removal of the arch of one of the vertebræ. The same clamp also gave support to a small apparatus by means of which delicate blades, cutting in planes parallel to the longitudinal axis of the body, could be adjusted in any desired position and then thrust with great precision vertically, horizontally, or obliquely through the substance of the spinal cord. These blades, which thus penetrated the cord longitudinally, served to isolate the portion of the cord to be divided and to protect the remainder from injury by compression or traction. As soon as the sections were made the blades and clamps were removed, the

1 Arbeiten aus der physiologischen Anstalt zu Leipzig, ix.
2 Arbeiten aus der physiologischen Anstalt zu Leipzig, v. 172.
3 Arbeiten aus der physiologischen Anstalt zu Leipzig, vi. 89.
4 Arbeiten aus der physiologischen Anstalt zu Leipzig, viii. 103.

wound carefully sewed up, and the results of the operation observed. The animals used in these experiments were rabbits, and the sections were all made at the level of the last dorsal vertebra. The author is particularly careful not to extend his conclusions to other animals or to other regions of the cord.

A systematic study was made of the effect of the mutilation, first, on the production of reflex actions due to irritation by pressure and electricity of the feet and ears of the animal; secondly, on the position of the limbs, both at rest and in movement; and, thirdly, on the production of movements in the hind limbs due to irritation by induced currents of the cord just below the calamus scriptorius. (These movements were found to consist in a series of alternate flexions and extensions of all the limbs, such as would be produced in powerful voluntary leaps. The same effect was produced by irritation of the cord anywhere above the origin of the sixth cervical nerves, which seems to show that the cervical cord is a centre for coördinated locomotive movements.)

The animal was usually killed about five hours after the operation, and the portion of the cord operated on removed and hardened in alcohol and chromate of ammonia. Microscopic sections were then made in the neighborhood of the wound, and that section which showed the most extensive divisions of the cord photographed with a magnifying power of twenty-five diameters. The original article contains a series of heliotype plates obtained in this way. The following figures represent in a general way the appearances shown in these plates, the shaded parts of the figures indicating the divided portions of the cord: —

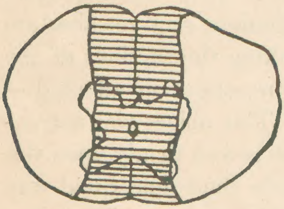

Fig. 1.

Fig. 1 represents the division of the anterior and posterior columns and nearly the whole of the gray substance. After this section, no disturbance of the transmission of motor or sensitive impressions through the cord can be detected. Pressure on any of the four extremities produces vigorous movements in all four limbs. The animal sits and moves in a perfectly normal manner. Irritation of the cervical cord causes at first the above-mentioned springing movements, and afterwards tetanic flexion of both hind legs.

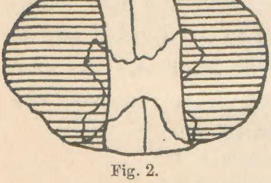

Fig. 2.

On the other hand, the section represented in Fig. 2 (which is the counterpart to Fig. 1) entirely prevents the transmission of impressions through that region of the cord. Irritation of one hind leg causes reflex movements of the same leg, or, if the irritation is a strong one, of the opposite leg also. Irritation of a fore leg causes movements in the anterior but not in the posterior part of the

body. Irritation of the cervical cord causes movements in all the muscles of the body except those of the hind legs.

Section of the posterior columns alone, as shown in Fig. 3, is absolutely without effect on the condition of the animal. All movements are executed in a perfectly normal manner. There is nowhere hyperæsthesia nor anæsthesia.

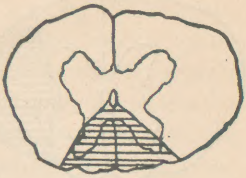

Fig. 3.

If, together with the posterior columns, portions of the lateral columns are also divided, as shown in Fig. 4, the effect is much the same, except that in springing the extension of the hind legs takes place with diminished force, while the flexion of those limbs is unaffected. A feeble irritation of the cervical cord causes a powerful tetanic flexion of all the joints of the hind legs.

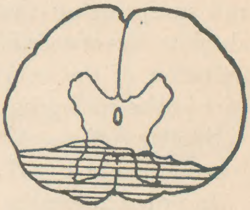

Fig. 4.

Division of the anterior columns with the adjoining portions of the lateral columns, as shown in Fig. 5, produces no effect except that in springing the animal extends the hind legs more powerfully than in the normal condition.

The result of these five series of experiments, showing that the channels of motor and sensitive impressions lie in the lateral and not in the anterior and posterior columns of the cord, is in opposition to the conclusions of many other investigators, and to the generally received opinion of physiologists. This contradiction is, according to the author, to be explained by the considerations, first, that similarity of results is to be expected only when the operations are performed on the same region of the cord, and secondly, that when partial sections of the cord are made without the use of protecting blades, as has been done by many investigators, the parts in the neighborhood of the section are necessarily more or less injured by pressure and traction.

Fig. 5.

Additional evidence that the lateral columns really contain the channels of motor and sensitive impressions is afforded by the result of sections such as are represented in Figs. 6 and 7. When the whole cord is divided except the left lateral column, as shown in Fig. 6, irritation of either hind foot causes movements of the anterior limbs, but the strength of the irritation which is sufficient to produce this effect is very much greater on the uninjured side of the body than on the opposite side. In other words, there is hyperæsthesia on the side of the injury. If, on the other hand, the strength of the irritation is measured which, when applied to the posterior limbs, is

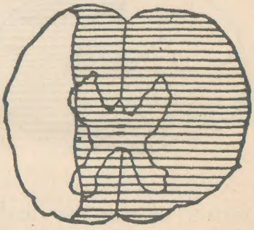

Fig. 6.

sufficient to produce reflex movements in the same limbs, it is found that the reverse is true, *i. e.*, there is hyperæsthesia on the uninjured side. Irritations applied to the fore limbs produce movements of both hind limbs, but the movements on the side of the injury are much feebler than those on the opposite side. In sitting, the animal does not support itself by the hind leg on the side of the injury, and in springing that limb is trailed behind. There is not, however, absolute loss of coördinated movement on the side of the injury, for strong irritation of the cervical cord causes the hind leg on that side to take part in the springing movements which are thus produced.

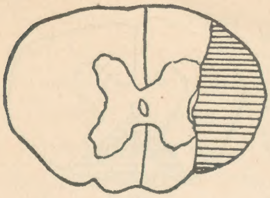

Fig. 7.

Similar effects follow the section of one of the lateral columns as represented in Fig. 7.

In order to localize still more definitely the course of nervous impressions in the lateral columns, more extensive sections of the cord were made. After a section of the whole cord except the posterior portion of the right lateral columns as shown in Fig. 8, irritation of the right foot causes only reflex movements of the hind limbs, while irritation of the left foot causes also movements of the fore limbs. There is complete loss of voluntary movements in the left hind leg, and irritation of the cervical cord has no effect on that limb, while on the opposite side the springing movements are well marked.

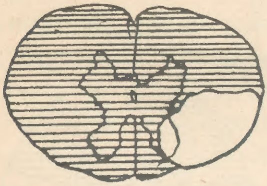

Fig. 8.

After a section such as is represented in Fig. 9, the movements produced by irritation of the hind legs are the same as those described in the case shown in Fig. 8. Irritation of the fore legs causes movements of the right, but not of the left hind leg. In sitting, the animal uses neither of its hind legs to support itself, but in springing makes some use of its right leg. Irritation of the cervical cord causes strong flexion of the right and extension of the left hind leg.

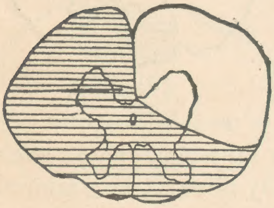

Fig. 9.

A still more extensive section is shown in Fig. 10. Even here, irritation of the hind leg on the side where the cord is completely destroyed causes movements in the anterior part of the body, but without any appearance of hyperæsthesia. Irritation of the fore limbs, however, causes no movement in the hind limbs, and irritation of the cervical cord produces no movement in the hind quarters except in the knee-joint of the leg on the side where a portion of the cord has been preserved.

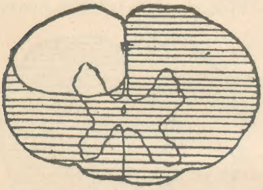

Fig. 10.

Although these experiments proved the possibility of dividing the whole cord, except a very small portion, without preventing the conduction of impressions through that portion, yet in view of the possible interference with the circulation in the retained part due to the division of so much of the substance of the cord, it seemed better to the author to seek to localize the channels of nerve-force in the different parts of the lateral columns by retaining portions of both instead of only one of the columns in question. Sections of this sort are shown in Figs. 11 and 12. The effect of such a section as is represented in Fig. 11 is the same as that described in connection with Fig. 9, except that both legs are now equally affected. In the same way Fig. 12 corresponds with Fig. 8.

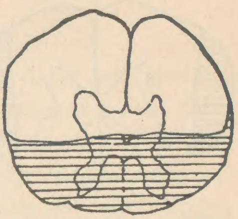

Fig. 11.

The general result of all the experiments illustrated by Figs. 8 to 12 inclusive may be stated as follows: —

Motor and sensitive nerve-fibres are found in all parts of the lateral columns.

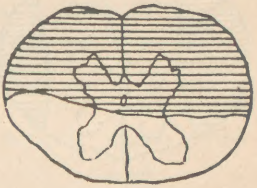

Fig. 12.

Sensitive fibres from both hind legs are found in each lateral column, but the fibres, in either column, which come from the leg on the opposite side are capable of producing stronger reflex movements in the anterior part of the body than are called forth by excitation of the fibres which come from the leg on the same side (crossed hyperæsthesia).

The centripetal fibres whose excitation produces these strong reflex movements, as well as those whose section on the opposite side gives occasion to them, lie in the middle third of the lateral columns, while the anterior and posterior thirds contain sensitive fibres which call forth movements of only moderate intensity in the anterior part of the body.

Motor fibres for both legs are found in each lateral column, but the motor fibres in different parts of these columns are called into activity in different ways. The reflex movements due to irritation of a fore leg can be excited in a hind limb only when the anterior half of the lateral column on the same side is preserved.

The coördinated movements of sitting and springing, and those produced by irritation of the cervical cord, are transmitted to each hind leg through the middle third of the lateral column on the same side.

Tetanus of both hind legs may be produced by irritation of the cord, even when the whole lateral column on one side has been destroyed; but if in addition to this the anterior two thirds of the lateral column on the other side has been divided, tetanus occurs only on the side where a portion of the cord is intact.

The author gives reasons, too lengthy for a place in this report, for regarding the crossed hyperæsthesia above alluded to as caused by the

division of the inhibitory fibres having their origin at the periphery and going to the centre of reflex action in the medulla. According to this view, the excito-reflex fibres of a limb have their course mainly, but not exclusively, in the opposite side, while the inhibitory reflex fibres lie chiefly on the same side, of the cord.

To effect a still more perfect localization of the channels of nervous impressions, sections were made such as are represented in Figs. 13 to 17. When only the external portions of the two lateral columns were divided, as shown in Fig. 13, the only effect observed was an interference with the movements of the feet. The toes were tetanically flexed, the left ankle-joint was extended, and the right one paralyzed.

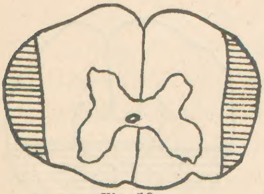

Fig. 13.

Instead of describing in detail the results of the sections represented in Figs. 14 to 17, it will be sufficient to state the conclusions which are to be drawn from his series of experiments. These are as follows: —

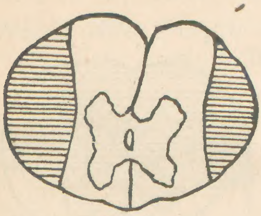

Fig. 14.

Motor and sensitive nerves are found mixed together in all parts of the lateral columns.

The fibres which preside over coördinated movements of the hind limbs, as well as those whose section causes hyperæsthesia on the side of the injury, lie in those parts of the lateral columns which are nearest to the gray substance. By uniting this result with that obtained by the sections shown in Figs. 8 to 12, it will be seen that the fibres in question lie in the inner half of the middle third of the lateral columns.

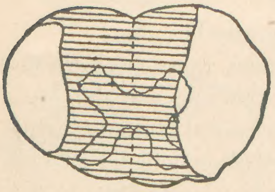

Fig. 15.

The motor nerve-fibres of the foot and lower leg seem to lie in the lateral columns externally to those of the thigh.

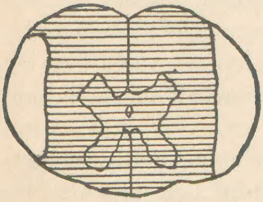

Fig. 16.

In all these experiments it was found that considerable portions of the lateral columns could be removed without affecting motion or sensibility in the leg, although the motor and sensitive character of the divided portion could be demonstrated with certainty. This would seem to indicate that the same muscle, or the same cutaneous surface, is represented in the spinal cord by fibres having various positions in the lateral columns. This agrees with the observations of Eckhard and others which show that two or three adjacent spinal roots send fibres to the same region of the body.

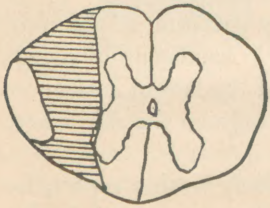

Fig. 17.

The main result of all these experiments, namely, that the lateral columns contain all the channels of motor and sensitive impressions, receives confirmation from the observations of Stilling on the areas of the cross-sections of the spinal nerves and of the columns of the spinal cord at different levels. A comparison of these areas shows that the lateral columns increase in size from below upwards, as if each successive spinal root contributed a certain proportion of its nerve fibres to their formation.

MUSCULAR SENSE.

The existence of sensitive nerves in muscles has been assumed by most physiologists as necessary to explain such phenomena as the feeling of muscular fatigue, the power of estimating the weight of objects, and the knowledge of the position of our limbs which enables us, consciously or unconsciously, to execute coördinated muscular movements. Although the sensitive nerves of the skin may aid to a certain extent in the performance of these functions, yet the part they play must be regarded as a very subordinate one. As conclusive evidence on this point may be mentioned the observation of Bernard [1] that the removal of the skin from the limbs of a frog does not essentially interfere with its powers of locomotion, while the section of the posterior roots of the sciatic plexus renders the animal's movements entirely uncontrolled and irregular (ataxia).

The principal opponent of the theory of muscular sensibility is Schiff,[2] who considers that our perception of the state of muscular contraction depends entirely upon a "central consciousness of innervation." In favor of this theory are the observations of Leyden [3] on ataxic and anæsthetic patients who still preserve the power of estimating the weight of objects. (Brown-Séquard's observations [4] that the channels of muscular sensibility do not decussate in the cord with the ordinary sensitive fibres are probably also to be interpreted as favoring this view.) Opposed to this hypothesis, on the other hand, are the experiments of Bernhardt,[5] who found that it made little or no difference in the accuracy with which weights could be estimated, whether the muscles were brought into contraction by an effort of the will or by electrical stimulation of the nerve. It seems probable, therefore, that the central consciousness of innervation plays an important though not an exclusive part in supplying information as to the condition of the muscles. The feeling of muscular fatigue depends, according to Schiff, not upon an affection of the sensitive nerves of muscles, but upon an

1 Système nerveux, i. 251.
2 Lehrbuch der Physiologie, i. 156.
3 Über Muskelsinn und Ataxie. Virchow's Archiv, Bd. 47, S. 321.
4 Archives de Physiologie, ii. 698.
5 Zur Lehre vom Muskelsinn. Archiv für Phsychiatrie, 1872.

interference with the circulation due to the limbs being kept too long in one position. In support of this view, Schiff makes the extraordinary statement that the same feeling of fatigue and pain which is experienced when the arm is held horizontally extended for fifteen minutes may be produced when the arm is *supported* in that position for the same length of time. Were this the case, we should, as has been well remarked, awake from sleep not refreshed and strengthened, but with violent pains in all our limbs. How the pain of muscular cramp is accounted for on this theory, Schiff does not explain.

Bernhardt also, in spite of his experiments above alluded to, is unwilling to admit the existence of nerves of muscular sense. He regards the estimation of weights as depending upon the central consciousness of innervation, the knowledge of the position of the limbs as derived through the Pacinian corpuscles, whose existence has been demonstrated on the articular nerves, and muscular pain (as in tetanus) as caused by pressure on nerves running through or over the muscles. This last hypothesis is of course quite inconsistent with the general law that the sensation caused by pressure on the trunk of a nerve is referred to its termination.

Anatomists as well as physiologists have brought forward reasons for attributing " sensitivity " to certain nerve-fibres distributed to muscles. Thus Bell, noticing that division of the facial nerve paralyzes the muscles of the face, although they also receive certain fibres from the trigeminus nerve, argued that certain sensations must have their origin in the muscles. Reichert,[1] in studying the terminations of nerves in the muscles of the frog, found a small number of fibres which ended very differently from the others, and suggested that they might be the sensitive muscular fibres. Kölliker[2] traced these nerve-fibres still farther, and discovered their terminations in the fascia surrounding the muscle. Odenius was still more successful in following out the ultimate ramifications of these fibres. His account of them is essentially the same as the one which will be given below.

Thus, although weighty anatomical and physiological reasons could be given for assuming the existence of centripetal nerve-fibres in muscles, yet the absolute demonstration of the fact was until recently wanting. This gap in our knowledge of the subject has been filled by Carl Sachs,[3] from whose treatise on the subject most of the above citations have been taken.

The experiments of this investigator were as follows: The reflex convulsions of frogs poisoned with strychnia and picrotoxine were used as an index of the irritation of sensitive nerves. The muscles of one of the hind limbs were rendered motionless by division of the anterior

[1] Reichert and Du Bois Reymond's Archiv, 1851, page 29.

[2] Microskopische Anatomie, ii. 240.

[3] Reichert and Du Bois Reymond's Archiv, 1874, pages 175, 491, 645.

roots on that side. The sartorius muscle of that side was then divided at its two extremities, and all its connections with the body, except the nerve, were severed. A thin plate of glass was then passed under it, and the preparation moistened with a drop of a three fourths per cent. solution of common salt. The muscle was then irritated by induced currents, and every contraction of the muscle was found to be accompanied by reflex convulsions of the rest of the body. It was thus shown that the sartorius muscle contains centripetal nerve-fibres whose irritation calls into activity the reflex centres of the spinal cord, but it was not shown that the contraction of the muscle, as such, is capable of stimulating the nerves in question, since in the above experiment the nerves themselves were irritated by the electrical current. It was therefore necessary to use some means of irritation which would act on the muscle and not on the nerve; ammonia is an irritant of this sort, and the sartorius muscle of the frog is particularly adapted to experiments of this kind, because its nervous distribution is limited to the central portion. The ammonia was applied by means of a piece of bibulous paper to a transverse section at one end of the muscle. A wave of contraction at once passed over the muscle, and reflex convulsions of the other limbs were immediately produced. It was thus shown that a contraction of a muscle is capable of stimulating centripetal nerves which are distributed through its substance and which enter the spinal cord by the posterior roots.

In order to obtain anatomical as well as physiological evidence of the existence of nerves of muscular sense, Waller's method of investigation was resorted to. This consists in dividing a nerve-root, or one of the component nerves of a nervous plexus, and studying the degeneration of the nerve-fibres which results from their separation from the nerve-centres. The course of the fibres thus divided can in this way be traced through the mixed nerve-trunks. If, for instance, six or eight weeks after division of the anterior roots of the nerves of a limb, it can be shown that the muscular nerves contain any undegenerated fibres, it may be assumed that these fibres are derived from the posterior roots. The application of this method to the sartorius muscle of frogs showed that the nerve supplying this muscle contains about twenty nerve-fibres, two of which only do not degenerate after section of the anterior roots. These two fibres may therefore be regarded as sensitive. (Schiff's[1] failure to find undegenerated fibres in the muscular nerves after section of the anterior roots is, according to Sachs, to be explained by the unsuitable methods of research adopted by that observer.) The converse experiment of dividing the posterior roots outside the ganglia did not give such definite results. The degeneration of the sensitive muscular nerves was found to be much slower and less complete than that of the motor nerves under similar circumstances.

[1] Lehrbuch der Physiologie, i. 159.

Still further evidence of the difference between the two sorts of nerve-fibres is afforded by the result of local irritation applied to the nerves in their course amongst the muscular fibres. The irritations were produced by induced currents sent through very fine platinum electrodes, which were applied close to the intra-muscular nerve-fibres as seen under the microscope. Experimenting in this way, Sachs found that in most cases a very feeble irritation was sufficient to cause a contraction of those muscular fibres to which the nerve in question supplied terminal plates, while the rest of the muscle was unaffected. Certain nerve-fibres, however, were found to which the irritation had to be applied with considerably increased intensity in order to produce a muscular contraction, and the contraction when produced was not limited to certain muscular fibres but extended over all the neighboring contractile substance. This would seem to show that the nerves in question had no motor function, but that the contraction was due to a general stimulation, by side currents, of the muscles and nerves in the neighborhood.

Histological investigations by Sachs have also shown a decided difference in the mode of distribution of the two sorts of nerves. While the motor nerves, subdividing dichotomously, end after a short course in the so-called terminal plates, the sensitive nerves, ramifying often dendritically, pursue an extended and isolated course over a large number of muscular fibres, and give rise to delicate non-medullated nucleated fibrillæ, which frequently anastomose with each other, and terminate partly in the connective tissue around the muscles, partly in the interstitial connective tissue, and partly as very fine branches surrounding the muscular fibres themselves.

The author also discusses the nature of the process by which the sensitive nerves are irritated in the living muscle. The feeling of fatigue he regards as due to a chemical change in the substance of the exhausted muscle (formation of lactic acid, etc.). The perception of a muscular contraction is probably due to a mechanical irritation of the sensitive nerves which run between and around the muscular fibres, and therefore follow from necessity their changes of form.